

JOURNAL OF ANIMAL SCIENCE

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J ANIM SCI 2011, 89:3859-3871.

doi: 10.2527/jas.2010-3810 originally published online July 25, 2011

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Bayesian estimation in maternally ancestral animal models for weaning weight of beef cattle¹

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ABSTRACT: The Bayesian approach was implemented for fitting several maternally ancestral models for weaning weight data of Angus calves. The goal was to evaluate to what extent genetic evaluation models with additive grand maternal effects (G), or with an ancestrally structured covariance matrix for maternal environmental effects (E), or with a sire \times year interaction (ISY), or combinations thereof (GE, GSY, ESY, GESY), redistribute the additive variability and reduce the negative magnitude of the additive correlation between direct and maternal effects (r_{AoAm}), when compared with the regular maternal animal model (I). All animals with records had known dams and maternal granddams. The sampling scheme induced low autocorrelations among all variables and tended to converge quickly. The signs of the estimates of r_{AoAm} were consistently negative for all models fitted. The magnitudes of the estimates of r_{AoAm} from models E, G, GE, ESY, and GESY were almost one-third of those from models I and ISY. Inclusion of the sire \times year interaction had some effect in reducing the negative magnitude of r_{AoAm} , but also reduced the size of the estimates of direct (h_o^2)

and maternal (h_m^2) heritabilities. In comparison, models E or G reduced the negative magnitude of r_{AoAm} by 0.50 units and produced more favorable estimates of h_o^2 and h_m^2 than models I and ISY. The estimate of h_o^2 from G was similar to the one from I; however, the estimated h_m^2 was 0.04 units greater, whereas the estimate of r_{AoAm} was much less negative (-0.21 vs. -0.71) than the respective estimates from I. The environmental correlation between the weaning weights of dams and their daughters (λ) was estimated to be -0.28 ± 0.03 in E and ESY, and -0.21 ± 0.03 in GE and GESY. Inclusion of the sire \times year interaction effect by itself did not have much of an impact in the reduction of the estimated magnitude of r_{AoAm} . Rank correlations among EBV for direct effects were larger than 0.94 and did not show any appreciable difference among models, whereas the rank correlation among maternal breeding values displayed differences in the ranking between I and the other models. Models E and ESY recovered the largest amount of total additive variability with maternal effects.

Key words: Bayesian estimation, beef cattle, grand maternal additive effect, maternal effect, sire \times year interaction, weaning weight

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J. Anim. Sci. 2011. 89:3859–3871
doi:10.2527/jas.2010-3810

INTRODUCTION

Even though genetic evaluation of weaning weight in beef cattle has been longstanding, both the model used for evaluation and the value of the additive covariance between direct and maternal effects (σ_{AoAm}) are still a matter of debate. The current maternal animal model (**MAM**) used in genetic evaluation includes additive direct and maternal effects, as well as independent maternal permanent environmental effects. However, Koch (1972) attempted to explain large negative estimates of σ_{AoAm} by the existence of an environmental correlation present in the phenotypic covariance between dam and offspring. At the same symposium, Willham (1972)

¹Funding for this research was provided by grants from the Secretaría de Ciencia y Técnica, Universidad de Buenos Aires (UBA; Secretaría de Ciencia y Técnica de la UBA G042/08); Agencia Nacional de Ciencia y Tecnología (1863/06) of Argentina, and CONICET (Proyecto de Investigación Plurianual 0833/2010). The authors thank Claudio Fioretti and Estancias y Cabaña Las Lilas for allowing the use of their data, and Eduardo Cappa, Sebastián Munilla Lequizamón, and Ana Birchmeier for many helpful discussions. Thanks are also due to Oscar Rhodas for help with manuscript preparation.

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Received December 22, 2010.

Accepted July 6, 2011.

proposed to include a genetic contribution to the maternal phenotype from all dams back in the pedigree through a maternal granddam effect. Years later, Robinson (1996) suggested that the estimate of σ_{AoAm} may be less negative if additional variation due to sires, in the form of a sire \times year or herd interaction, is accounted for. Parameter estimates obtained when fitting a correlation between maternal permanent environments provided by dams and their daughters (Quintanilla et al., 1999), or from additive grand maternal effects (Dodenhoff et al., 1999a), or from the sire \times herd interaction (Gutiérrez et al., 2006), support all 3 models because the MAM can properly account for all sources of variability if the information is complete. However, there is no indication of how these “enlarged” MAM redistribute the total additive and environmental variability among their dispersion parameters because the 3 models are not equivalent mixed models in the sense of Henderson (1985). Thus, the goal of this research is to evaluate how the fitting of several enlarged MAM affects the estimated (co)variances, when the information on dams and maternal granddams from the data is not limiting. A second objective is to show how to implement certain Bayesian Markov chain Monte Carlo (MCMC) algorithms for estimating the dispersion parameters of MAM.

Models

The data were analyzed with 8 different models. All of them included the following fixed effects: sex of calf (males, females), age of dam (2, 3, 4, 5 to 8, 9 or more years of age), contemporary groups (96 levels), and age of calf at weaning as a linear covariate. In order for the incidence matrix of the fixed effects (\mathbf{X}) to be of full rank, the solutions for the female calves and for the last level of age of dam were set to zero so that $\text{rank}[\mathbf{X}] = p = 102$. All models include random additive direct (\mathbf{a}_o) and maternal (\mathbf{a}_m) breeding values, as well as maternal environmental effects (\mathbf{e}_m) and the error term (\mathbf{e}_o). The model that results from including the grand maternal breeding values (\mathbf{a}_n ; Willham, 1972) in the MAM was denoted by G. Two different specifications of the covariance matrix for the \mathbf{e}_m vector were considered; the classic structure with independent environmental effects (I models), and the ancestrally correlated through the dam side covariance structure proposed by Quintanilla et al. (1999; E models). The model that includes a random sire \times year interaction effect (\mathbf{h} ; Robinson, 1996) was denoted as SY. There were $s = 1,062$ levels of the sire \times year interaction. The most general form of the model equation (model GESY) was equal to

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_o\mathbf{a}_o + \mathbf{Z}_m\mathbf{a}_m + \mathbf{Z}_n\mathbf{a}_n + \mathbf{Z}_p\mathbf{e}_m + \mathbf{Z}_{sy}\mathbf{h} + \mathbf{e}_o, \quad [1]$$

where \mathbf{y} is the vector of observations of order $7,229 \times 1$, \mathbf{X} is of order $7,229 \times 102$, and the vector of fixed effects $\boldsymbol{\beta}$ is of order 102×1 . The matrices \mathbf{Z}_o , \mathbf{Z}_m , and \mathbf{Z}_n (of order $7,229 \times 9,936$) relate \mathbf{a}_o , \mathbf{a}_m , and \mathbf{a}_n to \mathbf{y} , respectively; matrix \mathbf{Z}_p ($7,229 \times 2,444$) relates maternal environmental effects \mathbf{e}_m ($2,444 \times 1$) to \mathbf{y} ; \mathbf{Z}_{sy} ($7,229 \times 1,062$) relates \mathbf{h} ($1,062 \times 1$) to \mathbf{y} . Finally, \mathbf{e}_o ($7,229 \times 1$) is the vector of error terms. Expectations and variances of all random vectors in Eq. [1] are

$$\mathbf{E} \begin{bmatrix} \mathbf{a}_o \\ \mathbf{a}_m \\ \mathbf{a}_n \\ \mathbf{e}_m \\ \mathbf{h} \\ \mathbf{e}_o \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}; \quad \text{Var} \begin{bmatrix} \mathbf{a}_o \\ \mathbf{a}_m \\ \mathbf{a}_n \\ \mathbf{e}_m \\ \mathbf{h} \\ \mathbf{e}_o \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{Ao}^2 & \mathbf{A}\sigma_{AoAm} & \mathbf{A}\sigma_{AoAn} & 0 & 0 & 0 \\ \mathbf{A}\sigma_{AoAm} & \mathbf{A}\sigma_{Am}^2 & \mathbf{A}\sigma_{AmAn} & 0 & 0 & 0 \\ \mathbf{A}\sigma_{AoAn} & \mathbf{A}\sigma_{AmAn} & \mathbf{A}\sigma_{An}^2 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{E}\sigma_{Em}^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}_s\sigma_{SY}^2 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{I}_n\sigma_{Eo}^2 \end{bmatrix}. \quad [2]$$

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained because the data came from an existing database.

Data

Data were weaning weights ($n = 7,229$) from a purebred Angus herd, located at Pasteur, western Buenos Aires province, Argentina, collected from 1974 through 2008. The total number of animals in the pedigree (q) was 9,936, including 747 bulls and 3,404 cows. The number of cows mothering calves with records (d) was 2,444. The management of the herd and the selection procedures were described in Cantet et al. (1993). Calves born from embryo transplants or twins were discarded for all analyses. The average age at weaning was 194 ± 23 d, and the average weaning weight was 205.3 ± 40.3 kg. To correctly specify the genetic covariance matrix when grand maternal breeding values are included in the model, each animal with a record needs to have a known granddam (Dodenhoff et al., 1999b). Therefore, all analyses in the current research included only those calves whose sire, dam, and maternal granddam were identified. The total number of maternal granddams of calves with records was 1,905.

Matrix \mathbf{A} contains the additive relationship among all animals and was calculated using the Quaas algorithm (Quaas, 1976) to account for inbreeding. The dispersion parameters were the additive direct variance (σ_{Ao}^2), the additive maternal variance (σ_{Am}^2), the additive grand maternal variance (σ_{An}^2), the covariance between direct and maternal breeding values (σ_{AoAm}), the covariance between direct and grand maternal breeding values (σ_{AoAn}), the covariance between maternal and grand maternal breeding values (σ_{AmAn}), the maternal environmental variance (σ_{Em}^2), the correlation between maternal permanent environmental effects of dams and their daughters (λ), the sire \times year interaction variance (σ_{SY}^2), and the error variance (σ_{Eo}^2). Defining $\mathbf{a} = [\mathbf{a}'_o, \mathbf{a}'_m, \mathbf{a}'_n]'$ and $\mathbf{G}_o = \begin{bmatrix} \sigma_{Ao}^2 & \sigma_{AoAm} & \sigma_{AoAn} \\ \sigma_{AoAm} & \sigma_{Am}^2 & \sigma_{AmAn} \\ \sigma_{AoAn} & \sigma_{AmAn} & \sigma_{An}^2 \end{bmatrix}$ results in $\text{Var}(\mathbf{a}) = \mathbf{G}_o \otimes \mathbf{A}$. As in Quintanilla et al. (1999), the \mathbf{E} matrix was expressed as $\mathbf{E} = [g(\lambda)]$, assuming that the dam-daughter environmental relationship was constant across generations. Diagonal elements of matrix \mathbf{E} are ones, and off-diagonal elements \mathbf{E}_{ij} reflect the relationship between females i and j that are related through the maternal pathway by powers of λ , and zero otherwise. As an example, let dam i be the mother of dam j . Then, $\text{Cov}(\mathbf{e}_{mi}, \mathbf{e}_{mj}) = \lambda \sigma_{Em}^2$ with $|\lambda| < 1$. Alternatively, in models such as GSY, maternal environmental effects were independent, so that $\text{Var}(\mathbf{e}_m) = \mathbf{I}_{2444} \sigma_{Em}^2$. In model ESY, $\text{Var}(\mathbf{e}_m) = \mathbf{E} \sigma_{Em}^2$, the sire \times year interaction is included, and grand maternal effects are excluded. Alternatively, model ISY considers independent distributions for both the maternal environmental and the sire \times year interaction effects. Models GE, G, E, and I were based on models GESY, GSY, ESY and ISY, respectively, without the sire \times year interaction. The vectors \mathbf{e}_m and \mathbf{h} were assumed to be normally distributed and independent of each other, and both vectors are independent of the breeding values.

It should be emphasized that in contrast to the models with grand maternal effects (G, GE, and GESY), the vectors containing the total additive genetic effects (\mathbf{a}) in the maternal models (I, E, ISY, and ESY) have only 2 random effects instead of 3. As a consequence,

$$\mathbf{G}_o = \begin{bmatrix} \sigma_{Ao}^2 & \sigma_{AoAm} \\ \sigma_{AoAm} & \sigma_{Am}^2 \end{bmatrix}.$$

Bayesian Estimation Procedures

Dispersion parameters were estimated using a conjugate Bayesian approach, as in Cantet et al. (2004). Methods are presented for the most general model (GESY). It is assumed that, conditionally on all location effects (i.e., on $\boldsymbol{\theta} = [\boldsymbol{\beta}', \mathbf{a}', \mathbf{e}_m', \mathbf{h}']'$), and on the residual variance, data were a realization from the normal process:

$$\mathbf{y} | \boldsymbol{\theta}, \sigma_{Eo}^2 \sim N_n(\mathbf{W}\boldsymbol{\theta}, \mathbf{I}_n \sigma_{Eo}^2), \quad [3]$$

where $\mathbf{W} = [\mathbf{X} | \mathbf{Z}_o | \mathbf{Z}_m | \mathbf{Z}_n | \mathbf{Z}_p | \mathbf{Z}_{sy}]$. Hence, the likelihood of the observed data can be written as being proportional to

$$p(\mathbf{y} | \boldsymbol{\theta}, \mathbf{G}_o, \lambda, \sigma_{Em}^2, \sigma_{SY}^2, \sigma_{Eo}^2) \propto (\sigma_{Eo}^2)^{-\left(\frac{n}{2}\right)} \exp \left\{ -\frac{(\mathbf{y} - \mathbf{w}\boldsymbol{\theta})'(\mathbf{y} - \mathbf{w}\boldsymbol{\theta})}{2 \sigma_{Eo}^2} \right\}. \quad [4]$$

To reflect a prior state of uncertainty for the fixed effects and to obtain a proper posterior distribution (Hobert and Casella, 1996), we take the prior distribution of the $p \times 1$ vector $\boldsymbol{\beta}$ to be multivariate normal such that $\boldsymbol{\beta} \sim N_p(\mathbf{O}, \mathbf{K})$. Matrix \mathbf{K} is diagonal with large diagonal elements ($k_{ii} \geq 10^8$). This specification avoids having improper posteriors distributions in the mixed models. Also, the joint prior distribution of the additive genetic effects for the q animals is $\mathbf{a} | \mathbf{A}, \mathbf{G}_o \sim N_{lq}(\mathbf{O}, \mathbf{G}_o \otimes \mathbf{A})$, where l is the dimension of \mathbf{G}_o (3 in this case). Thus, the corresponding density can be written as

$$p(\mathbf{a} | \mathbf{A}, \mathbf{G}_o) \propto |\mathbf{G}_o|^{-\frac{q}{2}} \exp \left\{ -\frac{1}{2} \mathbf{a}'(\mathbf{G}_o^{-1} \otimes \mathbf{A}^{-1}) \mathbf{a} \right\}. \quad [5]$$

Additionally, the matrix \mathbf{G}_o follows a priori an inverted Wishart (IW) density: $\mathbf{G}_o \sim \text{IW}(\mathbf{G}_o^*, \nu_g)$, where \mathbf{G}_o^* is the prior covariance matrix and ν_g are the degrees of belief. More formally, we have

$$p(\mathbf{G}_o | \mathbf{G}_o^*, \nu_g) \propto |\mathbf{G}_o|^{-\frac{1}{2}(\nu_g + l + 1)} \exp \left\{ -\frac{1}{2} \text{tr}[\mathbf{G}_o^{*-1} \mathbf{G}_o^{-1}] \right\}. \quad [6]$$

A priori, the maternal permanent environmental variance has a scaled inverted χ^2 density so that

$$p(\sigma_{Em}^2 | \nu_{Em}, s_{Em}^2) \propto (\sigma_{Em}^2)^{-\left(\frac{\nu_{Em}}{2} + 1\right)} \exp\left\{-\frac{\nu_{Em} s_{Em}^2}{2 \sigma_{Em}^2}\right\} \quad [7]$$

with hyperparameters ν_{Em} , the degrees of belief, and s_{Em}^2 , the scale. The prior density for λ is a truncated normal so $-1 < \lambda < 1$, with a prior mean of -0.19 as estimated by Quintanilla et al. (1999). Also, the sire \times year interaction variance follows a priori a scaled inverted χ^2 density:

$$p(\sigma_{SY}^2 | \nu_{sy}, s_{sy}^2) \propto (\sigma_{SY}^2)^{-\left(\frac{\nu_{sy}}{2} + 1\right)} \exp\left\{-\frac{\nu_{sy} s_{sy}^2}{2 \sigma_{SY}^2}\right\}. \quad [8]$$

Prior parameters are the degrees of belief ν_{sy} and the scale s_{sy}^2 . Finally, the residual variance is assumed to follow a priori a scaled inverted χ^2 with density proportional to

$$p(\sigma_{Eo}^2 | \nu_{Eo}, s_{Eo}^2) \propto (\sigma_{Eo}^2)^{-\left(\frac{\nu_{Eo}}{2} + 1\right)} \exp\left\{-\frac{\nu_{Eo} s_{Eo}^2}{2 \sigma_{Eo}^2}\right\}. \quad [9]$$

Using the Bayes theorem, the joint posterior distribution of all parameters given the data can be expressed as

$$\begin{aligned} & p(\boldsymbol{\theta}, \mathbf{G}_0, \sigma_{Em}^2, \lambda, \sigma_{SY}^2, \sigma_{Eo}^2 | \mathbf{y}, \mathbf{G}_0^*, s_{Em}^2, s_{Eo}^2, \nu_g, \nu_{Em}, s_{sy}^2, \nu_{sy}, \nu_{Eo}) \propto \\ & p(\mathbf{y} | \boldsymbol{\theta}, \sigma_{Eo}^2) \times p(\boldsymbol{\beta} | \mathbf{K}) \times p(\mathbf{a} | \mathbf{G}_0) \times p(\mathbf{G}_0 | \nu_g, \mathbf{G}_0^*) \times p(\mathbf{e}_m | \lambda, \sigma_{Em}^2) \times \\ & p(\sigma_{Em}^2 | \nu_{Em}, s_{Em}^2) \times p(\lambda) \times p(\mathbf{h} | \sigma_{SY}^2) \times p(\sigma_{SY}^2 | \nu_{sy}, s_{sy}^2) \times p(\sigma_{Eo}^2 | \nu_{Eo}, s_{Eo}^2). \end{aligned} \quad [10]$$

Full Conditional Posterior Distributions

The full conditional posterior distributions are required to implement the Gibbs sampler. Let $\boldsymbol{\Omega}$ be the vector whose elements are the dispersion parameters of the model such that

$$\boldsymbol{\Omega}' = [\sigma_{Ao}^2, \sigma_{AoAm}, \sigma_{Am}^2, \sigma_{AoAn}, \sigma_{An}^2, \sigma_{AmAn}, \lambda, \sigma_{Em}^2, \sigma_{SY}^2, \sigma_{Eo}^2]';$$

and let $\boldsymbol{\Omega}_{-i}$ be similar to $\boldsymbol{\Omega}$ except for the i th element, which is removed from the entire vector of dispersion parameters. Then, the joint conditional posterior density of $\boldsymbol{\beta}$, \mathbf{a} , \mathbf{e}_m , and \mathbf{h} is

$$\left[\begin{array}{c} \boldsymbol{\beta} \\ \mathbf{a}_o \\ \mathbf{a}_m \\ \mathbf{a}_n \\ \mathbf{e}_m \\ \mathbf{h} \end{array} \right] | \boldsymbol{\Omega}, \mathbf{y} \sim N_{p+lq+d+s} \left(\left[\begin{array}{c} \hat{\boldsymbol{\beta}} \\ \hat{\mathbf{a}}_o \\ \hat{\mathbf{a}}_n \\ \hat{\mathbf{e}}_m \\ \hat{\mathbf{h}} \end{array} \right], \left[\begin{array}{cccccc} \mathbf{X}'\mathbf{X} + \mathbf{K}^{-1} & \mathbf{X}'\mathbf{Z}_o & \mathbf{X}'\mathbf{Z}_m & \mathbf{X}'\mathbf{Z}_n & \mathbf{X}'\mathbf{Z}_p & \mathbf{X}'\mathbf{Z}_{sy} \\ \mathbf{Z}_o'\mathbf{X} & \mathbf{Z}_o'\mathbf{Z}_o + \mathbf{A}^{-1}\mathbf{g}^{11} & \mathbf{Z}_o'\mathbf{Z}_m + \mathbf{A}^{-1}\mathbf{g}^{12} & \mathbf{Z}_o'\mathbf{Z}_n + \mathbf{A}^{-1}\mathbf{g}^{13} & \mathbf{Z}_o'\mathbf{Z}_p & \mathbf{Z}_o'\mathbf{Z}_{sy} \\ \mathbf{Z}_m'\mathbf{X} & \mathbf{Z}_m'\mathbf{Z}_o + \mathbf{A}^{-1}\mathbf{g}^{21} & \mathbf{Z}_m'\mathbf{Z}_m + \mathbf{A}^{-1}\mathbf{g}^{22} & \mathbf{Z}_m'\mathbf{Z}_n + \mathbf{A}^{-1}\mathbf{g}^{23} & \mathbf{Z}_m'\mathbf{Z}_p & \mathbf{Z}_m'\mathbf{Z}_{sy} \\ \mathbf{Z}_n'\mathbf{X} & \mathbf{Z}_n'\mathbf{Z}_o + \mathbf{A}^{-1}\mathbf{g}^{31} & \mathbf{Z}_n'\mathbf{Z}_m + \mathbf{A}^{-1}\mathbf{g}^{32} & \mathbf{Z}_n'\mathbf{Z}_n + \mathbf{A}^{-1}\mathbf{g}^{33} & \mathbf{Z}_n'\mathbf{Z}_p & \mathbf{Z}_n'\mathbf{Z}_{sy} \\ \mathbf{Z}_p'\mathbf{X} & \mathbf{Z}_p'\mathbf{Z}_o & \mathbf{Z}_p'\mathbf{Z}_m & \mathbf{Z}_p'\mathbf{Z}_n & \mathbf{Z}_p'\mathbf{Z}_p + \mathbf{E}^{-1} \frac{\sigma_{Eo}^2}{\sigma_{Em}^2} & \mathbf{Z}_p'\mathbf{Z}_{sy} \\ \mathbf{Z}_{sy}'\mathbf{X} & \mathbf{Z}_{sy}'\mathbf{Z}_o & \mathbf{Z}_{sy}'\mathbf{Z}_m & \mathbf{Z}_{sy}'\mathbf{Z}_n & \mathbf{Z}_{sy}'\mathbf{Z}_p & \mathbf{Z}_{sy}'\mathbf{Z}_{sy} + \mathbf{I}_s^{-1} \frac{\sigma_{Eo}^2}{\sigma_{SY}^2} \end{array} \right]^{-1} \right), \quad [11]$$

where

$$\left[\begin{array}{ccc} \mathbf{g}^{11} & \mathbf{g}^{12} & \mathbf{g}^{13} \\ \mathbf{g}^{21} & \mathbf{g}^{22} & \mathbf{g}^{23} \\ \mathbf{g}^{31} & \mathbf{g}^{32} & \mathbf{g}^{33} \end{array} \right] = \left[\begin{array}{ccc} \sigma_{Ao}^2 & \sigma_{AoAm} & \sigma_{AoAn} \\ \sigma_{AoAm} & \sigma_{Am}^2 & \sigma_{AmAn} \\ \sigma_{AoAn} & \sigma_{AmAn} & \sigma_{An}^2 \end{array} \right]^{-1} \sigma_{Eo}^2.$$

Finally, $\hat{\beta}$, $\hat{\mathbf{a}}_o$, $\hat{\mathbf{a}}_m$, $\hat{\mathbf{a}}_n$, $\hat{\mathbf{e}}_m$, and $\hat{\mathbf{h}}$ are the solutions of the following system of equations:

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} + \mathbf{K}^{-1} & \mathbf{X}'\mathbf{Z}_o & \mathbf{X}'\mathbf{Z}_m & \mathbf{X}'\mathbf{Z}_n & \mathbf{X}'\mathbf{Z}_p & \mathbf{X}'\mathbf{Z}_{sy} \\ \mathbf{Z}_o'\mathbf{X} & \mathbf{Z}_o'\mathbf{Z}_o + \mathbf{A}^{-1}\mathbf{g}^{11} & \mathbf{Z}_o'\mathbf{Z}_m + \mathbf{A}^{-1}\mathbf{g}^{12} & \mathbf{Z}_o'\mathbf{Z}_n + \mathbf{A}^{-1}\mathbf{g}^{13} & \mathbf{Z}_o'\mathbf{Z}_p & \mathbf{Z}_o'\mathbf{Z}_{sy} \\ \mathbf{Z}_m'\mathbf{X} & \mathbf{Z}_m'\mathbf{Z}_o + \mathbf{A}^{-1}\mathbf{g}^{21} & \mathbf{Z}_m'\mathbf{Z}_m + \mathbf{A}^{-1}\mathbf{g}^{22} & \mathbf{Z}_m'\mathbf{Z}_n + \mathbf{A}^{-1}\mathbf{g}^{23} & \mathbf{Z}_m'\mathbf{Z}_p & \mathbf{Z}_m'\mathbf{Z}_{sy} \\ \mathbf{Z}_n'\mathbf{X} & \mathbf{Z}_n'\mathbf{Z}_o + \mathbf{A}^{-1}\mathbf{g}^{31} & \mathbf{Z}_n'\mathbf{Z}_m + \mathbf{A}^{-1}\mathbf{g}^{32} & \mathbf{Z}_n'\mathbf{Z}_n + \mathbf{A}^{-1}\mathbf{g}^{33} & \mathbf{Z}_n'\mathbf{Z}_p & \mathbf{Z}_n'\mathbf{Z}_{sy} \\ \mathbf{Z}_p'\mathbf{X} & \mathbf{Z}_p'\mathbf{Z}_o & \mathbf{Z}_p'\mathbf{Z}_m & \mathbf{Z}_p'\mathbf{Z}_n & \mathbf{Z}_p'\mathbf{Z}_p + \mathbf{E}^{-1}\frac{\sigma_{Eo}^2}{\sigma_{Em}^2} & \mathbf{Z}_p'\mathbf{Z}_{sy} \\ \mathbf{Z}_{sy}'\mathbf{X} & \mathbf{Z}_{sy}'\mathbf{Z}_o & \mathbf{Z}_{sy}'\mathbf{Z}_m & \mathbf{Z}_{sy}'\mathbf{Z}_n & \mathbf{Z}_{sy}'\mathbf{Z}_p & \mathbf{Z}_{sy}'\mathbf{Z}_{sy} + \mathbf{I}_s^{-1}\frac{\sigma_{Eo}^2}{\sigma_{SY}^2} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{\mathbf{a}}_o \\ \hat{\mathbf{a}}_m \\ \hat{\mathbf{a}}_n \\ \hat{\mathbf{e}}_m \\ \hat{\mathbf{h}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}_o'\mathbf{y} \\ \mathbf{Z}_m'\mathbf{y} \\ \mathbf{Z}_n'\mathbf{y} \\ \mathbf{Z}_p'\mathbf{y} \\ \mathbf{Z}_{sy}'\mathbf{y} \end{bmatrix}. \quad [12]$$

The full conditional posterior distribution of maternal environmental effects was

$$p(\sigma_{Em}^2 | \boldsymbol{\theta}, \Omega_{-i}, \mathbf{y}) \propto (\sigma_{Em}^2)^{-\left(\frac{d + \nu_{Em}}{2} + 1\right)} \exp\left[-\frac{\mathbf{e}_m' \mathbf{E}^{-1} \mathbf{e}_m + \nu_{Em} s_{Em}^2}{2 \sigma_{Em}^2}\right]. \quad [13]$$

This is a scaled inverted χ^2 density with $\tilde{\nu}_{Em} = d + \nu_{Em}$ degrees of belief and scale parameter $\tilde{s}_{Em}^2 = \frac{\mathbf{e}_m' \mathbf{E}^{-1} \mathbf{e}_m + \nu_{Em} s_{Em}^2}{\nu_{Em} + d}$; that is, $\sigma_{Em}^2 | \boldsymbol{\theta}, \Omega_{-i}, \mathbf{y} \sim \chi^2(\tilde{\nu}_{Em}, \tilde{s}_{Em}^2)$. For the variance of sire \times year interaction effects, the full conditional posterior distribution was

$$p(\sigma_{SY}^2 | \boldsymbol{\theta}, \Omega_{-i}, \mathbf{y}) \propto (\sigma_{SY}^2)^{-\left(\frac{s + \nu_{SY}}{2} + 1\right)} \exp\left[-\frac{\mathbf{h}'\mathbf{h} + \nu_{SY} s_{SY}^2}{2 \sigma_{SY}^2}\right]. \quad [14]$$

Again, a scaled inverted χ^2 density with $\tilde{\nu}_{sy} = s + \nu_{sy}$ degrees of belief and scale parameter $\tilde{s}_{sy}^2 = \frac{\mathbf{h}'\mathbf{h} + \nu_{sy} s_{sy}^2}{\nu_{sy} + s}$; that is, $\sigma_{SY}^2 | \boldsymbol{\theta}, \Omega_{-i}, \mathbf{y} \sim \chi^2(\tilde{\nu}_{sy}, \tilde{s}_{sy}^2)$. The full conditional posterior density of the residual variance was proportional to

$$p(\sigma_{Eo}^2 | \boldsymbol{\theta}, \Omega_{-i}, \mathbf{y}) \propto (\sigma_{Eo}^2)^{-\left(\frac{\tilde{\nu}_{Eo}}{2} + 1\right)} \exp\left[-\frac{\tilde{\nu}_{Eo} \tilde{s}_{Eo}^2}{2 \sigma_{Eo}^2}\right], \quad [15]$$

where $\tilde{\nu}_{Eo} = \nu_{Eo} + n$ and $\tilde{s}_{Eo}^2 = \frac{(\mathbf{y} - \mathbf{W}\boldsymbol{\theta})'(\mathbf{y} - \mathbf{W}\boldsymbol{\theta}) + \nu_{Eo} s_{Eo}^2}{\tilde{\nu}_{Eo}}$. Thus, the density was equal to $\sigma_{Eo}^2 | \boldsymbol{\theta}, \Omega_{-i}, \mathbf{y} \sim \chi^2(\tilde{\nu}_{Eo}, \tilde{s}_{Eo}^2)$.

Sampling of G_0 Using Differential Degrees of Belief

To sample from the posterior conditional density of \mathbf{G}_0 , let \mathbf{S}_g be

$$\mathbf{S}_g = \mathbf{a}'(\mathbf{G}_0^{-1} \otimes \mathbf{A}^{-1})\mathbf{a} = \begin{bmatrix} \mathbf{a}_o'\mathbf{A}^{-1}\mathbf{a}_o & \mathbf{a}_o'\mathbf{A}^{-1}\mathbf{a}_m & \mathbf{a}_o'\mathbf{A}^{-1}\mathbf{a}_n \\ \mathbf{a}_m'\mathbf{A}^{-1}\mathbf{a}_o & \mathbf{a}_m'\mathbf{A}^{-1}\mathbf{a}_m & \mathbf{a}_m'\mathbf{A}^{-1}\mathbf{a}_n \\ \mathbf{a}_n'\mathbf{A}^{-1}\mathbf{a}_o & \mathbf{a}_n'\mathbf{A}^{-1}\mathbf{a}_m & \mathbf{a}_n'\mathbf{A}^{-1}\mathbf{a}_n \end{bmatrix}.$$

Thus,

$$p(\mathbf{G}_0 | \boldsymbol{\theta}, \Omega_{-i}, \mathbf{y}) \propto |\mathbf{G}_0|^{-\frac{1}{2}(\nu + q + l + 1)} \exp\left\{-\frac{1}{2}tr[\mathbf{G}_0^{-1}(\mathbf{S}_g + \mathbf{G}_0^{*-1})]\right\},$$

which can be recognized as the kernel of an $l \times l$ scaled IW distribution, with degrees of belief equal to $\nu + q$ and scale matrix $\mathbf{S}_g + \mathbf{G}_0^{*-1}$:

$$\mathbf{G}_0 \mid \boldsymbol{\theta}, \Omega_{-i}, \mathbf{y} \sim \text{IW}_l \left[\nu + q, (\mathbf{S}_g + \mathbf{G}_0^{*-1})^{-1} \right].$$

To reflect differences in uncertainty for the prior variances and covariances of the additive genetic effects, the elements of the genetic covariance matrix \mathbf{G}_0 were sampled individually using a generalized IW distribution (**GIW**, Brown, 2001), as suggested by Daniels and Pourahmadi (2002). The GIW distribution is based on applying the Bartlett decomposition of a matrix and involves a larger set of hyperparameters than the inverted Wishart. Let

$$\mathbf{G} = \begin{bmatrix} g_{11} & g_{12} & g_{13} \\ g_{21} & g_{22} & g_{23} \\ g_{31} & g_{32} & g_{33} \end{bmatrix} = \begin{bmatrix} g_{11} & \mathbf{g}_1 \\ \mathbf{g}_1' & \mathbf{G}_{-1} \end{bmatrix},$$

so that \mathbf{g}_1 is a 2×1 vector and \mathbf{G}_{-1} a 2×2 matrix. Then, the Bartlett decomposition of \mathbf{G} is such that $\mathbf{G} = \mathbf{T} \boldsymbol{\Delta} \mathbf{T}'$ with

$$\begin{aligned} \boldsymbol{\Delta} &= \begin{bmatrix} g_{11} & 0 \\ 0 & \begin{bmatrix} g_{22} & g_{23} \\ g_{32} & g_{33} \end{bmatrix} - \begin{bmatrix} g_{12} \\ g_{13} \end{bmatrix} (g_{11})^{-1} \begin{bmatrix} g_{12} & g_{13} \end{bmatrix}' \end{bmatrix} \\ \mathbf{T} &= \begin{bmatrix} 1 & 0 \\ \begin{bmatrix} (g_{11})^{-1} g_{12} \\ (g_{11})^{-1} g_{13} \end{bmatrix} & \mathbf{I}_2 \end{bmatrix}. \end{aligned} \quad [16]$$

The decomposition allows using the properties of the GIW, so that g_{11} , $\begin{bmatrix} (g_{11})^{-1} g_{12} \\ (g_{11})^{-1} g_{13} \end{bmatrix}$, and

$$\begin{bmatrix} g_{22} & g_{23} \\ g_{32} & g_{33} \end{bmatrix} - \begin{bmatrix} g_{12} \\ g_{13} \end{bmatrix} (g_{11})^{-1} \begin{bmatrix} g_{12} & g_{13} \end{bmatrix}'$$

are distributed as an inverted χ^2 , a multivariate normal, and an IW, respectively. The idea is to sample g_{11} first, and then g_{12} conditionally on g_{11} . Next, g_{22} is sampled conditionally on g_{11} and g_{12} , and so on. This formulation allows using different degrees of belief for all additive variances. A full description of the algorithm and its characteristics will be published elsewhere. Degrees of belief were used such that σ_{Ao}^2 received 2 times more than σ_{Am}^2 and 6 times more than σ_{An}^2 .

To increase the comparability of the estimates across all fitted models in the current research and with estimates published elsewhere, results are presented in terms of heritabilities instead of additive variances, additive correlations instead of additive covariances, and ratio of variances, so that

$$\begin{aligned} h_o^2 &= \frac{\sigma_{Ao}^2}{\sigma^2}; & h_m^2 &= \frac{\sigma_{Am}^2}{\sigma^2}; & h_n^2 &= \frac{\sigma_{An}^2}{\sigma^2}; \\ c^2 &= \frac{\sigma_{Em}^2}{\sigma^2}; & c_{SY} &= \frac{\sigma_{SY}^2}{\sigma^2} \\ r_{AoAm} &= \frac{\sigma_{AoAm}}{\sqrt{\sigma_{Ao}^2 \sigma_{Am}^2}}; & r_{AoAn} &= \frac{\sigma_{AoAn}}{\sqrt{\sigma_{Ao}^2 \sigma_{An}^2}}; \\ r_{AmAn} &= \frac{\sigma_{AmAn}}{\sqrt{\sigma_{Am}^2 \sigma_{An}^2}}, \end{aligned}$$

with σ^2 being the phenotypic variance of the corresponding model. For each model, total heritability (h_T^2) was calculated using the estimated values of the genetic (co)variance components as $h_T^2 = \sigma_T^2 / \sigma^2$, where σ_T^2 is the total additive variance (Dickerson, 1947). For MAM, σ_T^2 was taken from Willham (1972) as $\sigma_{Ao}^2 + 1.5\sigma_{AoAm} + 0.5\sigma_{Am}^2$.

Sampling of λ

Instead of sampling λ using the Metropolis-Hastings as in Quintanilla et al. (1999), we sampled the parameter from a truncated normal density. Whereas Chib (1993) is the first reference to the topic, Heringstad et al. (2003) applied the sampler to a threshold model for data on clinical mastitis. The method is based on partitioning the vector \mathbf{e}_m in such a way that $\mathbf{e}_m = [\mathbf{e}_{mD}', \mathbf{e}_{mP}']'$, similar to the reduced animal model (Quaas and Pollak, 1980), wherein individuals are considered as parents or nonparents. The subvectors result from ordering the effects such that dams of cows with progeny, in \mathbf{e}_{mD} , antecede cows that are not mothers of dams, in \mathbf{e}_{mP} . Then, the density was $p(\mathbf{e}_{mD}, \mathbf{e}_{mP} | \mathbf{E}_\lambda) \sim N_d(\mathbf{0}, \mathbf{E}_\lambda \sigma_{Em}^2)$. To proceed with the algorithm, the first step was to fit the regression

$$\mathbf{e}_{mP} = \lambda \mathbf{S} \mathbf{e}_{mD} + \boldsymbol{\varepsilon},$$

where \mathbf{S} relates \mathbf{e}_m effects of dams to the effects of their mothers. The error of the regression ($\boldsymbol{\varepsilon}$) was such that $\boldsymbol{\varepsilon} \sim N_d(\mathbf{0}, \mathbf{I} \sigma_\varepsilon^2)$ with $\sigma_\varepsilon^2 = (1 - \lambda) \sigma_{Em}^2$. The regression error variance σ_ε^2 was sampled from the density $p(\sigma_\varepsilon^2 | \mathbf{e}_m, \lambda) \sim \boldsymbol{\varepsilon}' \boldsymbol{\varepsilon} \chi_{d-2}^{-2}$ (Heringstad et al., 2003). The sampling of λ was from the truncated normal conditional posterior density

$$p(\lambda | \mathbf{e}_{mD}, \mathbf{e}_{mP}, \sigma_\varepsilon^2) \sim N_{TR}[E(\lambda), \text{Var}(\lambda)] \quad [17]$$

with parameters

$$\begin{aligned} \mathbf{E}(\lambda) &= (\mathbf{e}_{mD}' \mathbf{S}' \mathbf{S} \mathbf{e}_{mD})^{-1} \mathbf{e}_{mD}' \mathbf{S}' \mathbf{e}_{mP} \\ \text{Var}(\lambda) &= (\mathbf{e}_{mD}' \mathbf{S}' \mathbf{S} \mathbf{e}_{mD})^{-1} \sigma_\varepsilon^2. \end{aligned}$$

The truncation in the parameter space of λ was to ensure that the resulting matrix \mathbf{E} be positive-definite. It was found by trial and error that when $-0.30 < \lambda < -0.01$ for models E and ESY, and $-0.25 < \lambda < -0.01$ for models GE and GESY, matrix \mathbf{E} was positive definite (i.e., $\mathbf{E} > 0$). An accept-reject algorithm was used to sample from a 2-sided truncated normal distribution, as proposed by Robert (1995).

MCMC Sampling Scheme

The Gibbs sampler was implemented using a long chain of length 100,000. At each iteration, the Gibbs algorithm proceeds by first sampling $\boldsymbol{\beta}$, \mathbf{a} , \mathbf{e}_m , and \mathbf{h} from the updated full conditional distribution [11]. Next, the error variance is sampled from [15], the variance σ_{Em}^2 from [13], and the parameter λ from [17]. The algorithm continues with the sampling of \mathbf{G}_0 from a GIW, using the Bartlett decomposition [16]. Finally, the variance σ_{SY}^2 is sampled from [14]. Jensen et al. (1994) explained the implementation of the Gibbs sam-

pler for MAM with independent maternal environmental effects in detail. Nevertheless, for models that included matrix \mathbf{E} , the sampling of λ was as proposed by Chib (1993). Following Geyer (1992), the first 2,000 iterates (2%) were discarded due to burn-in, and the remaining iterates were used to estimate the marginal densities. Convergence was assessed by visual appraisal of the running means plus the control of whether the statistics of Geweke (1992) were within the range $(-2, 2)$, as implemented in the Bayesian Output Analysis package (BOA; Smith 2003). Evidence of convergence within the number of iterates as indicated above was obtained for all models except for ISY, which required lengthening the chain. Posterior statistics were calculated using the program POSTGIBBSF90 from the package BLUPF90 (Misztal et al., 2002). All remaining calculations were performed with different programs written in FORTRAN. To evaluate if considerable re-ranking of the animals occurs, Spearman correlations for the direct and maternal breeding values of the 8 models were calculated.

RESULTS AND DISCUSSION

As the sampling scheme induced low autocorrelations for all variables (data not shown), Gibbs iterates converged quickly for all parameters with the exception of c_{SY} in model ISY, which required further iterations. Table 1 displays the posterior means with their SD and the 95% highest posterior density intervals (**95% HPD**) of the genetic and environmental dispersion parameters for all models.

All marginal densities were unimodal, tended to be symmetric, and point estimators of mean, mode, and median were similar for most parameters. Therefore, only means are reported in Table 1. Although parameters λ and c_{SY} displayed asymmetric marginal posterior densities (Figures 1 and 2), the estimated values of the posterior means, medians, and modes were similar too. None of the 95% HPD for h_o^2 , h_m^2 , h_n^2 , r_{AoAm} , r_{AmAn} , λ , c^2 , c_{SY} , or σ_{Eo}^2 included 0, which suggests that these parameters are different from zero. Estimates of h_o^2 were consistently larger than h_m^2 in all models, and the latter estimates were larger than those of h_n^2 . Ranges of mean estimates across models were 0.11 to 0.19 for h_o^2 , 0.08 to 0.15 for h_m^2 , and 0.10 to 0.11 for h_n^2 . Cantet et al. (1993) estimated $h_o^2 = 0.12$ and $h_m^2 = 0.03$, from a subset of 935 records of the current data set using REML. In Angus, Dodenhoff et al. (1999a) estimated $h_o^2 = 0.22$, $h_m^2 = 0.11$, and $h_n^2 = 0.06$. In the current research, the estimates with the largest magnitude for h_o^2 and h_m^2 were observed in models E and ESY, and the least in model ISY (see the discussion of r_{AoAm} below). Estimates of h_m^2 from models E, G, and GE were larger than the estimates from the customary maternal animal model I, whereas the opposite was true for the parameter c^2 : the greatest value was found for models I and ISY. These results agree with those of Meyer (1992), Robinson

Table 1. Posterior means with their SD and the 95% highest posterior density intervals (in parentheses) of all dispersion parameters for the 8 models¹

Model	Parameter										
	h_o^2	h_m^2	h_n^2	r_{AoAm}	r_{AoAn}	r_{AmAn}	λ	c^2	c_{SY}	σ_{Eo}^2	h_T^2
I	0.16 ± 0.02 (0.12 to 0.20)	0.09 ± 0.02 (0.05 to 0.14)	*	-0.71 ± 0.08 (-0.86 to -0.52)	*	*	*	0.15 ± 0.02 (0.12 to 0.18)	*	495.99 ± 7.34 (481.75 to 510.49)	0.077
E	0.19 ± 0.00 (0.18 to 0.20)	0.15 ± 0.00 (0.14 to 0.16)	*	-0.21 ± 0.08 (-0.37 to -0.05)	*	*	-0.28 ± 0.03 (-0.30 to -0.20)	0.07 ± 0.01 (0.05 to 0.09)	*	487.31 ± 6.56 (474.57 to 500.32)	0.213
G	0.16 ± 0.00 (0.15 to 0.17)	0.13 ± 0.00 (0.12 to 0.14)	0.11 ± 0.00 (0.10 to 0.11)	-0.21 ± 0.00 (-0.37 to -0.05)	0.09 ± 0.10 (-0.10 to 0.29)	0.19 ± 0.10 (-7.10^{-3} to 0.40)	*	0.07 ± 0.00 (0.06 to 0.09)	*	482.09 ± 6.45 (469.68 to 494.95)	0.181
GE	0.17 ± 0.00 (0.16 to 0.18)	0.13 ± 0.00 (0.13 to 0.14)	0.10 ± 0.00 (0.09 to 0.11)	-0.21 ± 0.08 (-0.37 to -0.05)	0.10 ± 0.10 (-0.11 to 0.30)	0.20 ± 0.11 (-6.10^{-3} to 0.40)	-0.21 ± 0.04 (-0.25 to -0.08)	0.05 ± 0.00 (0.03 to 0.06)	*	483.88 ± 6.49 (471.36 to 496.76)	0.187
ISY	0.11 ± 0.02 (0.06 to 0.17)	0.08 ± 0.02 (0.05 to 0.13)	*	$-0.63_{\text{w}} \pm 0.13$ (-0.85 to -0.33)	*	*	*	0.15 ± 0.02 (0.11 to 0.18)	0.03 ± 0.01 (0.01 to 0.05)	497.64 ± 7.41 (483.15 to 512.23)	0.062
ESY	0.19 ± 0.00 (0.18 to 0.20)	0.15 ± 0.00 (0.14 to 0.16)	*	-0.21 ± 0.08 (-0.37 to -0.05)	*	*	-0.28 ± 0.03 (-0.30 to -0.20)	0.07 ± 0.01 (0.05 to 0.09)	0.01 ± 0.00 (2.10^{-2} to 0.03)	484.68 ± 6.64 (471.77 to 497.82)	0.210
GSY	0.16 ± 0.00 (0.15 to 0.17)	0.13 ± 0.00 (0.12 to 0.14)	0.10 ± 0.00 (0.09 to 0.11)	-0.21 ± 0.08 (-0.37 to -0.05)	0.10 ± 0.10 (-0.11 to 0.30)	0.20 ± 0.11 (-7.10^{-3} to 0.41)	*	0.07 ± 0.00 (0.06 to 0.09)	0.01 ± 0.00 (1.10^{-3} to 0.02)	479.92 ± 6.53 (467.25 to 492.78)	0.181
GESY	0.17 ± 0.00 (0.16 to 0.18)	0.13 ± 0.00 (0.12 to 0.14)	0.10 ± 0.00 (0.09 to 0.11)	-0.21 ± 0.08 (-0.37 to -0.05)	0.10 ± 0.10 (-0.11 to 0.30)	0.20 ± 0.10 (-0.11 to 0.41)	-0.21 ± 0.04 (-0.25 to -0.08)	0.05 ± 0.00 (0.03 to 0.06)	0.01 ± 0.00 (5.10^{-4} to 0.02)	481.69 ± 6.52 (469.11 to 494.60)	0.186

¹ h_o^2 = direct heritability; h_m^2 = maternal heritability; h_n^2 = grand maternal heritability; r_{AoAm} = genetic correlation between direct and maternal effects; r_{AoAn} = genetic correlation between direct and maternal effects; r_{AmAn} = genetic correlation between maternal permanent environmental effects of a dam and its daughters; c^2 = fraction of variance due to maternal permanent environmental effects; c_{SY} = proportion of phenotypic variance accounted for by sire × year interaction variance; σ_{Eo}^2 = residual variance; h_T^2 = heritability for total additive effects. I = uncorrelated maternal environmental effects; E = correlated maternal environmental effects; G = grand maternal additive effects; SY = sire × year interaction.

*Parameters that do not correspond to the model.

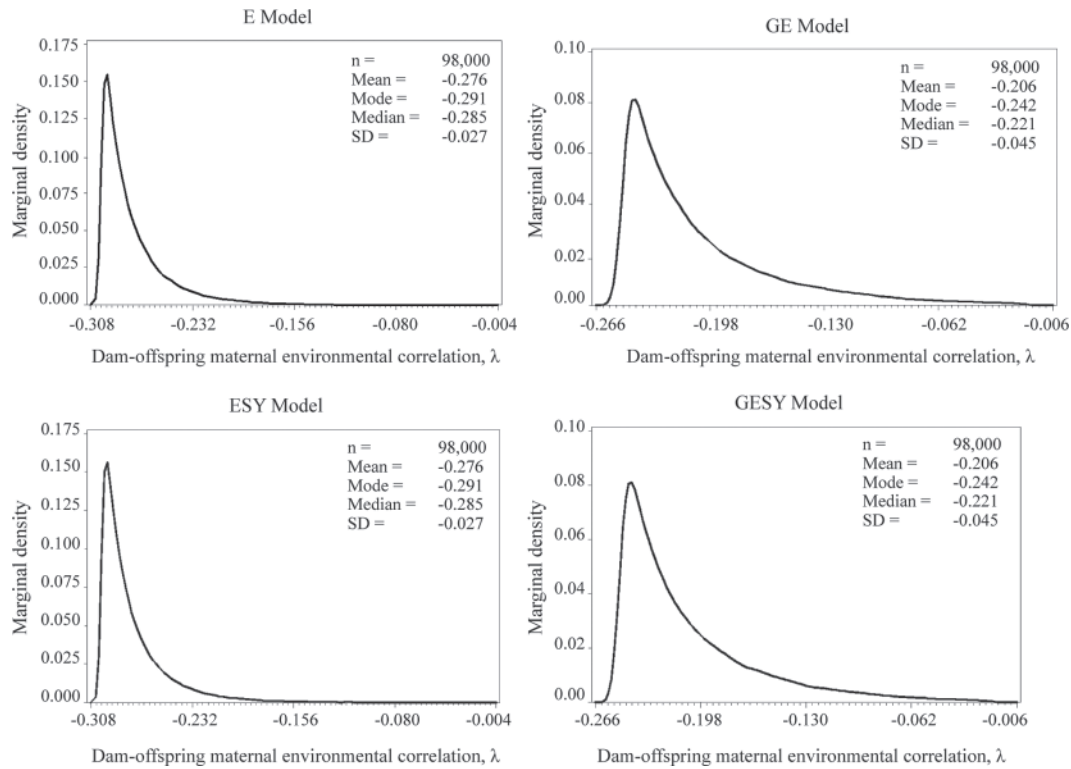


Figure 1. Marginal densities of the dam-offspring maternal environmental correlation (λ) for models E, ESY, GE, and GESY (E = correlated maternal environmental effects; G = grand maternal additive effects; SY = sire \times year interaction).

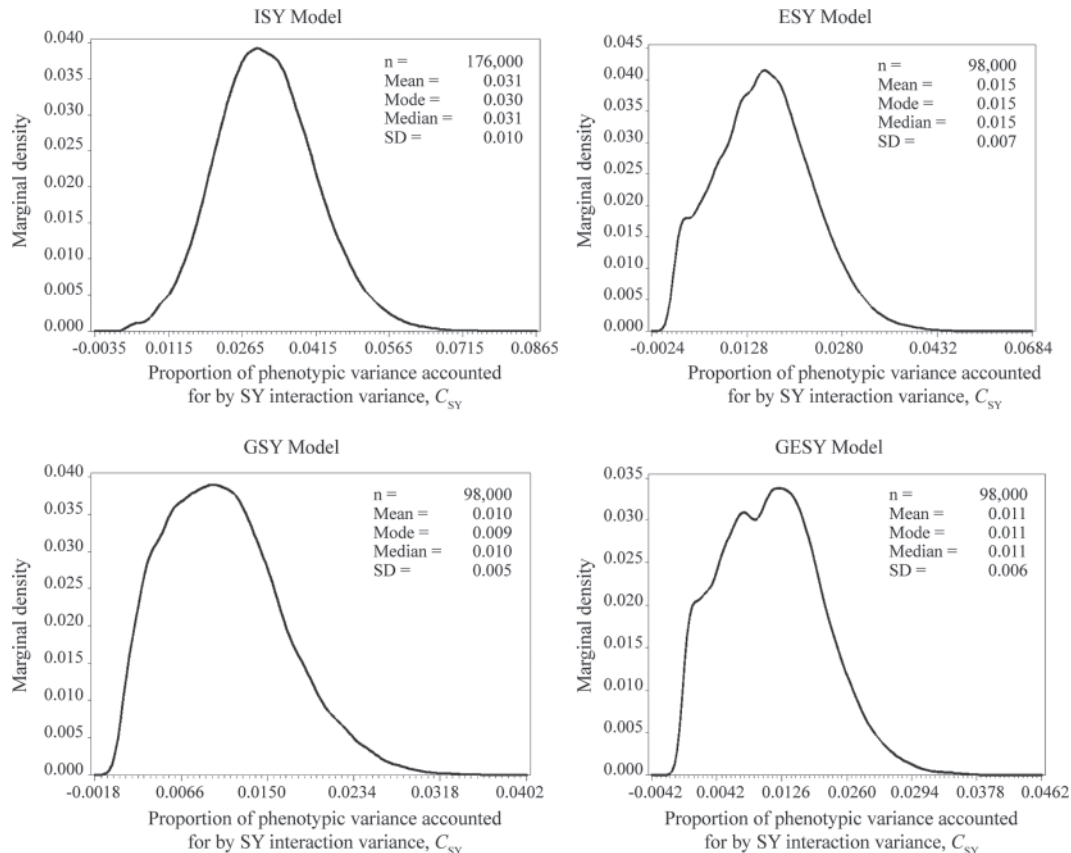


Figure 2. Marginal densities of the proportion of phenotypic variance accounted for by sire \times year interaction variance (c_{SY}) obtained in the models with a sire \times year interaction (I = uncorrelated maternal environmental effects; E = correlated maternal environmental effects; G = grand maternal additive effects; SY = sire \times year interaction).

Table 2. Rank correlations between estimated breeding values for direct weaning weight (above diagonal) and between estimated breeding values for maternal weaning weight (below diagonal)¹

Model	I	E	G	GE	ISY	ESY	GSY	GESY
I	1	0.965	0.972	0.971	0.985	0.960	0.958	0.968
E	0.854	1	0.995	0.996	0.941	0.998	0.986	0.995
G	0.851	0.976	1	0.999	0.950	0.993	0.990	0.998
GE	0.845	0.978	0.999	1	0.948	0.994	0.990	0.998
ISY	0.965	0.922	0.918	0.913	1	0.943	0.952	0.950
ESY	0.842	0.999	0.975	0.977	0.920	1	0.990	0.996
GSY	0.818	0.968	0.992	0.991	0.910	0.972	1	0.994
GESY	0.835	0.976	0.998	0.999	0.911	0.977	0.994	1

¹ I = uncorrelated maternal environmental effects; E = correlated maternal environmental effects; G = grand maternal additive effects; SY = sire \times year interaction.

(1996), Dodenhoff et al. (1998), Quintanilla et al. (1999), and Iwaisaki et al. (2005) and support the idea that under model I, h_m^2 is underestimated, whereas c^2 is overestimated.

As is customary with almost all estimates of the parameter, the sign of r_{AoAm} was consistently negative throughout all models fitted in this study. The magnitudes of the estimates of r_{AoAm} from models involving either grand maternal effects or nonindependent maternal environmental effects (E, G, GE, ESY, and GESY) were almost one-third of the magnitudes of the estimates from models I and ISY. Inclusion of the sire \times year interaction had some effect in reducing the magnitude of r_{AoAm} , but also reduced the size of the estimates of h_o^2 and h_m^2 . In comparison, models including λ or grand maternal additive effects reduced the magnitude of r_{AoAm} in 0.50 units while producing more favorable estimates of h_o^2 and h_m^2 than models I and ISY.

Grand Maternal Additive Effects

The values of the estimates of h_n^2 suggest that grand maternal effects exist for weaning weight in this Angus population. The estimate of h_o^2 from model G was similar to the one from model I; however, the estimated h_m^2 was 0.04 units greater, whereas the estimate of r_{AoAm} was much less negative (-0.21 vs. -0.71) than the respective estimates from model I. Similarly, Dodenhoff et al. (1998, 1999a,b) attempted to fit the model of Willham (1972) with additive and permanent environmental grand maternal effects in several data sets from different purebreds and composites, using average information REML. Convergence of this complex model occurred in 8 out of 25 data sets. With the exception of a Hereford line selected for yearling weight (Dodenhoff et al., 1998), estimates of r_{AoAm} for weaning weight from the model including grand maternal effects were less negative than those estimates of r_{AoAm} from the MAM. Positive correlations were observed between maternal and grand maternal genetic effects (r_{AmAn}), contrary to the expectation of Willham (1972). However, our results were consistent in all models including G effects (Table 1, models GE, GSY, and GESY). Finally, the

parameter r_{AoAn} was estimated to be negligible, now in agreement with Willham (1972) who doubted that a nonzero r_{AoAn} exists. The total heritability (h_T^2) estimated from model G was greater than from model I due to the decreased magnitude of the covariance between direct and maternal effects (σ_{AoAm}) obtained from model G. The same situation was present in model E. We did not find problems of convergence when estimating the model with grand maternal genetic effects, as those reported by Dodenhoff et al. (1998, 1999a,b). It is unlikely that the difference in performance in both investigations is due to the use of a different method of estimation, but rather due to the data structure: number of dams and maternal granddams with records, number of progeny per dam, number of generations of recorded data, and relationships between relatives related from the maternal side (Gerstmayr, 1992; Maniatis and Pollott, 2003). On the other hand, we did not attempt to include the grand maternal permanent environmental effects to avoid excessive overparameterization of models.

Models with Environmental Effects

Fitting a sire \times herd-year interaction and uncorrelated maternal permanent environmental effects in the ISY model resulted in smaller estimates of h_o^2 and h_m^2 and less negative estimates of r_{AoAm} when compared with the estimates from model I, which does not include the interaction term. The result is consistent with the findings of Dodenhoff et al. (1999b). The most probable reason why h_o^2 and h_m^2 decrease when including a sire \times year interaction is due to removing part of the variability accounted by sires, which is present in σ_{Ao}^2 and σ_{Am}^2 . Moreover, the correlation of sampled values between the chains of parameters σ_{Ao}^2 and σ_{SY}^2 was the greatest in magnitude and had a negative sign (-0.58 in model ISY). Additionally, the confounding between additive direct effects and the sire \times year interaction was evident while attempting to fit the interaction with a correlated covariance structure using the additive relationships among sires, as the estimate of σ_{Ao}^2 , and thus of h_o^2 , went to zero (data not shown). As expected, esti-

mates of c^2 were not affected by the inclusion of the sire \times year effect into a model, such as I. The same situation was observed by Baschnagel et al. (1999) for weaning weights of Swiss Angus cattle when a random sire \times herd interaction was in the model. The sire \times year variance represented 1 to 3% of the phenotypic variance in the current data, a result in agreement with Lee and Pollak (1997) who reported $c_{SY} = 0.03$ in Simmentals, whereas Dodenhoff et al. (1999b) obtained estimates of c_{SY} in the range of 0.02 to 0.10. The estimate of h_T^2 was the smallest of all analyses, suggesting that there is not much to gain in terms of total heritability when including the sire \times year interaction if E or G effects are already in the model. A word of caution should be noted at this point. Because the analysis performed here used data from just 1 herd, a sire \times herd interaction was impossible to fit. It is likely that the causes for the existence of a sire \times year interaction in a single herd are different than those causing sire \times herd interactions in a multiple-herd data set (for example, nonadditive genetic effects), so the 2 types of interactions do not necessarily redistribute the genetic variation similarly. However, because variance due to sires explains one-quarter of the additive variance, inclusion of any interaction involving sires would somehow reduce additive variance.

With regard to the environmental antagonism between the weaning weights of dams and their daughters, the posterior means of λ in the present study were -0.28 ± 0.03 in models E and ESY, and -0.21 ± 0.03 in models GE and GESY. Although the marginal posterior densities of λ were not symmetric in the 4 models, we chose to report the posterior means because they were not dissimilar to the posterior medians and modes. Here, the estimated values of λ were consistently negative, and in the range of -0.25 to -0.30 in all models (Figure 1). These results can be interpreted as evidence of a negative relationship between maternal permanent environmental effects of females in 2 consecutive generations, for weaning weight in beef cattle. Cantet et al. (1988) estimated λ to be -0.25 in Herefords, whereas Quintanilla et al. (1999) obtained an estimate of -0.19 for Bruna dels Pirineus. The latter authors also found that assuming independence between maternal environmental effects of 2 generations resulted in biased estimates of all the (co)variance components. Iwaisaki et al. (2005) compared REML estimates of genetic and environmental (co)variance components for weaning weight from Gelbvieh and Limousin calves, while trying different fixed values of the correlation between maternal permanent environmental effects ($\lambda = 0, -0.10, -0.20, -0.30$). As the value of λ became more negative, r_{AoAm} was reduced from -0.25 to -0.17 in Gelbvieh, and from -0.59 to -0.52 in Limousin. Additionally, Iwaisaki et al. (2005) found in both breeds that models with nonzero estimates for λ had smaller values (better fit) of the negative log-likelihood than the model with $\lambda = 0$. The smaller estimate of c^2 may be the result of taking into account the environmental correlation

between maternal effects of ancestrally related dams instead of assuming them independent.

Models that Combine Genetic and Environmental Effects

It is worth noting that pairs of models that differ in the inclusion of the sire \times year interaction (i.e., E and ESY, G and GSY, and GE and GESY) displayed identical posterior means. Thus, the variability associated with the sire \times year interaction was explained by the maternal environmental effects ancestrally correlated (E), the grand maternal additive effects (G), or both set of variables (GE). When the sire \times year interaction was fitted simultaneously with the maternal permanent environmental effects (model ESY), and also with the grand maternal effects (model GESY), the posterior marginal densities of c_{SY} displayed irregular shapes when compared with the posterior density of c_{SY} from model ISY (Figure 2). This suggests that when models ESY and GESY were fitted to the data, there was little information available to estimate all dispersion parameters simultaneously and accurately. Alternatively, Figure 2 is suggestive of a lack of information on c_{SY} if λ is included in the model. Therefore, it does not seem to be useful to include both an ancestrally structured covariance matrix for maternal environmental effects combined with the sire \times year interaction in this Angus data set because they are competing for information. Moreover, the sire \times year interaction effect by itself did not have much of an impact in the reduction of the estimated magnitude of r_{AoAm} .

Correlations Between EBV

Rank correlations between estimated breeding values from the 8 models are given in Table 2. Correlations between estimated breeding values for direct weaning weight (above diagonal) were larger than 0.94 in all cases. In fact, they did not show any significant difference between models. With respect to maternal breeding values, there were differences in the ranking between model I and the rest, except for ISY. However, models E, G, GE, ESY, GSY, and GESY did not differ among them. These findings suggest that for maternal breeding values, considering the correlation between maternal permanent environmental effects of 2 adjacent generations, the grand maternal genetic effects, or both effects would have a similar effect in the genetic evaluations of animals.

Recovery of Total Additive Variation with Maternal Effects

The last column in Table 1 displays the estimated values of h_T^2 for each model. Estimates of h_T^2 from models E, G, GE, ESY, GSY, and GESY were greater than the estimates from models I and ISY, basically because of the decreased negative magnitude of σ_{AoAm} . Models E

and ESY recovered the largest amount of total additive variability with maternal effects.

Algorithmic and Convergence Issues

A distinctive issue in the current research is the efficiency and effectiveness of the samplers used to obtain successful estimates of the dispersion parameters from the complex overparameterized models with ancestral maternal effects. In particular, we would like to mention the scalar sampling of the (co)variances in \mathbf{G}_0 using the GIW distribution, and the Gibbs sampler for λ using the algorithm by Chib (1993). The latter algorithm does not require tuning parameters as the Metropolis scheme that was originally implemented by Quintanilla et al. (1999).

One of the problems in the Bayesian analyses of maternally influenced traits is the selection of the degrees of belief for the IW distribution of the additive genetic effects, a density that has a single degree of belief for all (co)variance components: usually there is less information for σ_{Am}^2 than for σ_{Ao}^2 . Moreover, this problem is aggravated in models that additionally include an additive effect of the granddam because usually there is much less information for σ_{An}^2 than σ_{Am}^2 . Thus, the individual sampling with differential degrees of belief for the additive (co)variances via the GIW distribution resulted in successful fits of structurally complex maternal animal models.

General

The goal of this research was to detect which overparametrized models provided the smallest magnitude in the estimates of r_{AoAm} with the greatest estimates of h_o^2 and h_m^2 . As discussed previously, inclusion of a sire \times year interaction resulted in a reduction of h_o^2 and h_m^2 with a slight reduction in the negative magnitude of r_{AoAm} . More advantageous was to include either grand maternal effects or nonindependent permanent environmental effects. These 2 effects are probably a reflection of the negative phenotypic relationship observed between the dam weaning weight and the weaning weight of her progeny (Kress and Burfening, 1972; Johnsson and Morant, 1984). As a result, cows that were exposed to greater amounts of milk before weaning because of overfeeding themselves became below average mothers (Koch, 1972), a phenomenon sometimes referred to as the fatty udder syndrome. As a consequence, the level of milk production offered to the calf alternates among the different generations of dams. Viewed as an additive genetic process, this is the maternal granddam effect (Willham, 1972) present in models G, GE, GSY, and GESY. However, “the relationship between maternal environmental effects provided by dam and daughters,” implying “a recurrent relationship between maternal environments contributed by all dams related in the female pathway” (Quintanilla et al., 1999) is the

recursive environmental effect involved in models E, GE, ESY, and GESY. Given that the inclusion of λ (model E) resulted in a reasonably small magnitude in the estimate of r_{AoAm} with the greatest estimates of h_o^2 and h_m^2 , and that fitting additive grand maternal effects (model G) increases the number of breeding values to predict and the computing complexity of the estimation problem, model E is recommended for genetic evaluation purposes. Moreover, it can be fitted with little additional computation effort when compared with the classic MAM.

An alternative parameter that enters into the covariance between offspring and dam was discussed by Koch (1972), Willham (1972), Foulley and Lefort (1978), and Bijma (2006), so that we have

$$\text{Cov}(O, D) = \frac{1}{2} \sigma_{Ao}^2 + \frac{5}{4} \sigma_{AoAm} + \frac{1}{2} \sigma_{Am}^2 + \sigma_{EoEm}.$$

The last term, σ_{EoEm} , represents “the environmental covariance between the direct effect of the dam, expressed in her own phenotype, and the maternal effect of the dam, expressed in the phenotype of her offspring” (Bijma, 2006). Contrary to the inclusion of λ , which when multiplying σ_{Em}^2 appears only in the covariance between the record of a cow and those of her daughters that became dams with calves with records, the covariance σ_{EoEm} enters into the covariance between any dam with own record and those data from all its progeny, either female or male. Bijma (2006) observed that “environmental covariances between dam and offspring are likely to be a general phenomenon,” rather than a “special case such as the fatty udder syndrome in beef cattle.” Indeed, the nature of the process may be different in pluriparous when compared with uniparous species. The covariance σ_{EoEm} was assumed to be zero in the current research because the residual covariance displays a complex correlation structure between the error effects (\mathbf{e}_o) and a set of random effects in the model (\mathbf{e}_m), when cows which have their own weaning weights recorded have more than 1 progeny with data. Bijma (2006) showed how to fit a moving average correlation structure to data on which each dam with records has only one progeny with data. Preliminary research on the estimation of σ_{EoEm} on this Angus data set has been reported by Munilla Leguizamón and Cantet (2010), and final results will be published elsewhere.

Conclusions

Inclusion of ancestrally maternal effects, either additive grand maternal or nonindependent environmental effects of dams related from the female pathway, reduced the negative magnitude of the additive correlation between direct and maternal effects, in a beef cattle data set where a sizable fraction of granddams of animals with phenotypic records was known. The meaningful reduction of the negative magnitude of r_{AoAm} and the recovery of total additive variance favors

the use of nonindependent environmental effects for genetic evaluation of weaning weight in beef cattle.

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